Carboniferous and Permian species of the cyclostome bryozoan *Corynotrypa* Bassler, 1911 and their clonal propagation

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Synopsis

Two rare cyclostome bryozoans are redescribed: *Corynotrypa thomasi* Condra & Elias from the L. Carboniferous of Alabama and U. Carboniferous of Nebraska, and *C. voigtiana* (King) from the U. Permian of Durham and Thuringia. Colonies consist of adnate, uniserial branches of simple, elongate-pyriform zooids. Lateral branches arise sporadically as distolateral buds. Colony growth commences from groups of 2–4 radiating zooids united at their narrow proximal ends. None of these zooids possesses a protoecium diagnostic of an ancestrula, and indications of damage suggest that these colony origins may be the products of fragmentation and regeneration rather than of larval settlement. The occurrence of clones of colonies (ramets) arising from fragmentation may have been common in *Corynotrypa*. Preliminary morphological evidence indicates that late Palaeozoic corynotrypids may be less closely related to primitive post-Palaeozoic cyclostomes than are some early Palaeozoic crownoporids.

Introduction

One of the outstanding current problems in bryozoan evolution concerns the phylogenetic relationships between Palaeozoic and post-Palaeozoic stenolaemates. A widely held view is that the dominant Palaeozoic stenolaemate orders (Trepostomata, Cryptostomata, Fenestrata, Cystoporata) became extinct at the end of the Permian, and that all post-Palaeozoic stenolaemates are cyclostomes, descended from Palaeozoic cyclostomes, a comparatively minor group until the Jurassic. This view is now known to be incorrect in at least one respect; unequivocal trepostomes survived the Permo–Triassic extinction event and are found in Triassic deposits from various parts of the world (e.g. Fritz 1961, Morozova 1969, Smit 1976, Sakagami & Sakai 1979). In addition, morphological similarities between various groups of post-Palaeozoic cyclostomes and Palaeozoic trepostomes, cryptostomes and cystoporates, previously attributed to convergent evolution, are reinterpreted by Boardman (1981, 1984) as probable indicators of phylogenetic affinity. If any of these interpretations are correct then post-Palaeozoic cyclostomes are polyphyletic, descended in part from Palaeozoic trepostomes, cryptostomes, cystoporates and cyclostomes.

Cyclostomes of late Palaeozoic age clearly have an important bearing on the ancestry of post-Palaeozoic cyclostomes. However, the late Palaeozoic record of cyclostomes is unfortunately very meagre. Excluding hederellids, which are of doubtful bryozoan affinity (Brood 1975), the only late Palaeozoic cyclostomes thus far described are a few corynotrypids. These include Devonian species of *Corynotrypa* from Canada, France and Poland described by Bassler (1911) and Kiepura (1973), and Devonian to Permian species of the erect genus *Lagenosypho* from several parts of the world described by Langer (1980). Only two post-Devonian species of *Corynotrypa* are known, *C. thomasi* Condra & Elias from the Carboniferous of the USA, and *C. voigtiana* (King) from the Permian of Britain and Germany. The purpose of this paper is to redescribe these two rare species based on a study of type specimens, and augmented by some new material of superior preservation. Particular attention is focused on colony propagation in these and other species of *Corynotrypa*.

Abbreviations of specimen repositories are as follows: British Museum (Natural History), BMNH; Nebraska Geological Survey (University of Nebraska State Museum, Lincoln), NGS; University College Galway, UCG; Naturwissenschaftliches Museum Coburg, NMC.

Systematic descriptions

Order CYCLOSTOMATA Busk, 1852

Suborder PALEOTUBULOPORINA Brood, 1973

Family CORYNOTRYPIDAE Dzik, 1981

Genus *CORYNOTRYPA* Bassler, 1911

TYPE SPECIES. *Hippothoa delicatula* James 1878. Middle Ordovician of N. America and Esthonia, U. Ordovician of N. America (Bassler 1911).

REMARKS. *Corynotrypa* has encrusting colonies composed of uniserial branches of simple zooids, narrow proximally but broadening distally, terminated by a circular or subcircular aperture sometimes with a slight peristome. Unlike most other uniserial cyclostomes, *Corynotrypa* lacks calcified interior walls and the chambers of successive zooids are in spatial continuity via the pore-like structure formed by the narrow proximal parts of the zooids (Boardman & Cheetham 1973, Brood 1975).

Bassler (1911) recognized three subdivisions of *Corynotrypa* according to the shape of the zooecia: a *C. delicatula* subdivision with zooecia narrow throughout their lengths, a *C. inflata* subdivision with zooecia initially very narrow but becoming bulbous distally, and a *C. dissimilis* subdivision with zooecia moderately broad throughout their lengths. However, Bassler acknowledged the existence of intermediate morphologies and the two species described herein lie somewhere between the *C. delicatula* and *C. dissimilis* subdivisions.

RANGE. Middle Ordovician–Upper Permian. The only two post–Palaeozoic records of *Corynotrypa* cited by Bassler (1911) are erroneous; *C. smithii* (Phillips) from the Middle Jurassic of Yorkshire is a bioimmured ctenostome assigned to *Arachnidium* by Taylor (1978), and *C. tenuichorda* (Ulrich & Bassler) from the Palaeocene of Virginia was later reassigned to the cheilostome genus *Hippothoa* by Canu & Bassler (1933: 71).

Corynotrypa thomasi Condra & Elias 1944

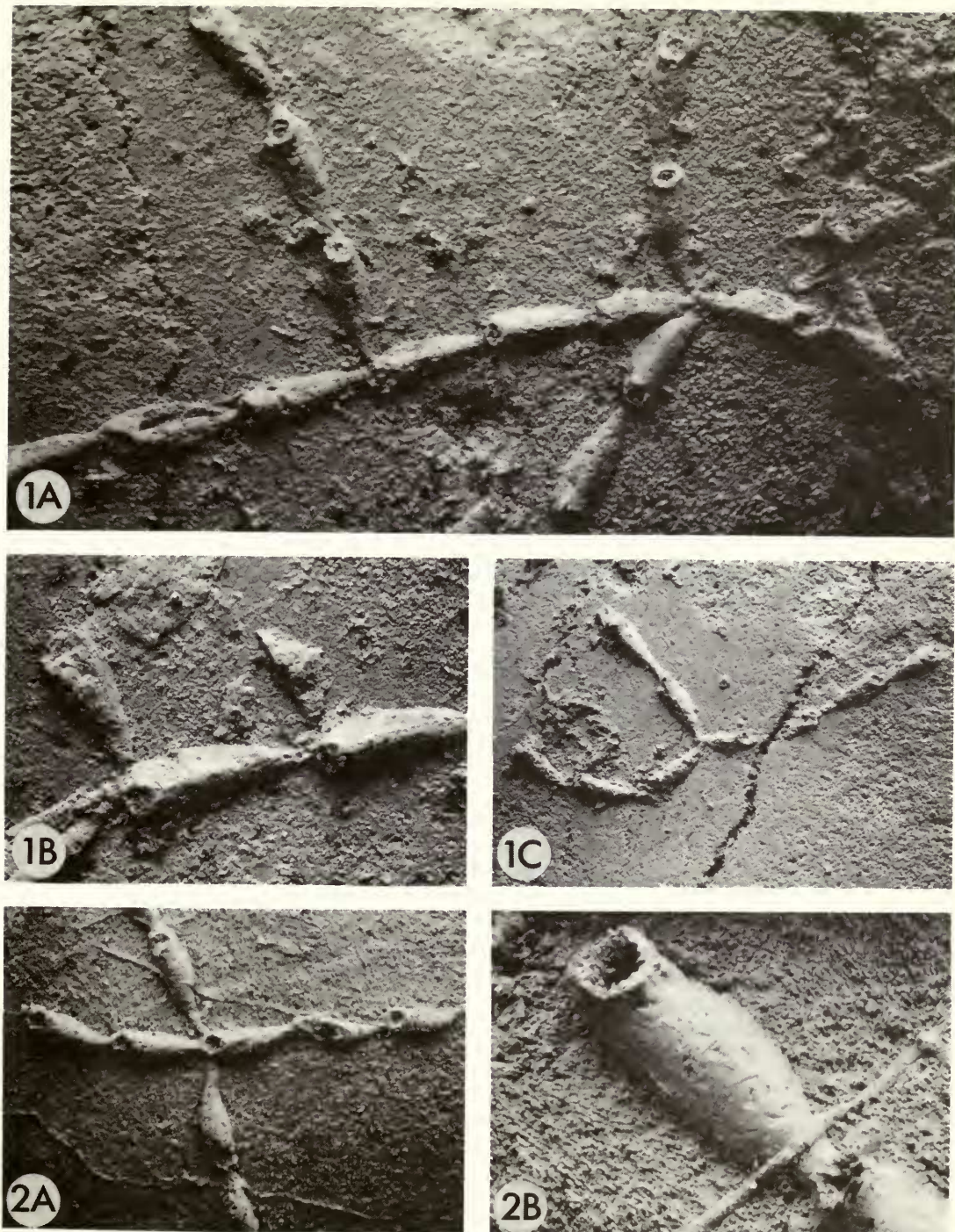1944 *Corynotrypa thomasi* Condra & Elias: 538; pl. 91, figs 1–4.

HOLOTYPE. NGS 256. Spring Branch Limestone Member, Lecompton Formation, Shawnee Group, Pennsylvanian (U. Carboniferous). Snyderville Quarry, 3 miles west and 1 mile north of Nehawka, Nebraska, U.S.A. Encrusting the interior of a valve of *Pinna peracuta* (*fide* Condra & Elias 1944).

OTHER MATERIAL. BMNH PD6023, PD6216, Bangor Limestone (lower), Chesterian, Mississippian (L. Carboniferous). Fox Trap (Sec. 31, T5S, R10W), Old Bethel Quadrangle, Colbert County, Alabama, U.S.A. (see Thomas, Mack & Waters 1980 for locality details). PD6023 encrusts the brachiopod *Coelidium explanatum* and was collected by P. D. Taylor during October 1982; PD6216 encrusts a bellerophontid collected by F. K. McKinney.

Condra & Elias (1944) mention two specimens additional to their holotype. NGS 257 from the type locality is missing (R. K. Pabian *in litt.*, May 1983). A specimen thought to be NGS 258, from the Dover Limestone (Wabaunsee Series, Pennsylvania) of Pawnee City, Nebraska, no longer bears any trace of the *C. thomasi* colony that was figured by Condra & Elias (1944: pl. 91, figs 3–4).

DESCRIPTION. Colonies are entirely encrusting and consist of branches of uniserially-arranged zooids sparsely covering the substratum (Fig. 1A). Colony branches tend to be gently curved

Figs 1–2 *Corynotrypa thomasi* Condra & Elias. Fig. 1, NGS 256; Spring Branch Limestone Member, Lecompton Formation, Shawnee Group, Pennsylvanian (U. Carboniferous); Snyderville Quarry, Nehawka, Nebraska, U.S.A. 1A, part of large colony, ×35; 1B, two daughter branches forming as distolateral buds, ×50; 1C, small colony on same substrate, ×20. Fig. 2, BMNH PD6023; Bangor Limestone (lower), Chesterian, Mississippian (L. Carboniferous); Fox Trap, Colbert County, Alabama, U.S.A. 2A, paired lateral daughter branches, ×25; 2B, well-preserved zooid lacking pseudopores and crossed by the thread of a vinellid, ×95.
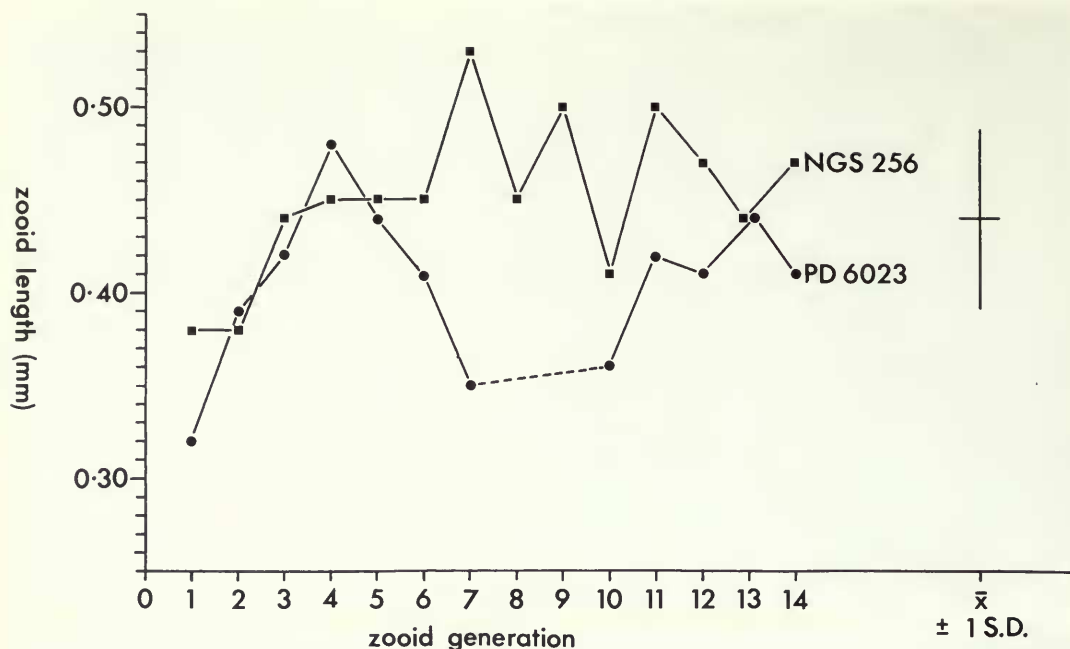
Fig. 3   Astogenetic variation in zooid length in colonies of *Corynotrypa thomasi* Condra & Elias from the U. Carboniferous of Nebraska (NGS 256) and L. Carboniferous of Alabama (BMNH PD6023). Successive zooids were measured outwards from the smallest zooids present in the apparent colony origins shown in Figs 6A and 7A. A slight gradient of astogenetic change seems to be present in both colonies. The bar at the right of the figure indicates the mean value and standard deviation calculated from 102 measurements of zooid length in *C. thomasi* (Table 1).

owing to a combination of the slightly curved shape of many zooids and non-alignment of the longitudinal axes of successive zooids. Division of branches is infrequent and lacks any obvious regularity of pattern. Daughter branches are lateral branches arising from the distolateral budding of a new zooid from a zooid on the parent branch (Fig. 1B). Fifteen per cent or fewer of zooids in each colony give rise to such a distolateral bud, which are usually single but occasionally paired, one either side of the zooid (Fig. 2A). Lateral branches diverge from the parent branch at about 60°–90°. Few branch intersections are observed and the result of intersections are variable; overgrowth of the earlier-formed branch followed an intersection in NGS 256, whereas cessation of growth was the apparent outcome of an intersection in BMNH PD6023 (cf. Gardiner & Taylor 1982). Branches may be traced proximally to a colony origin (Figs 6, 7), consisting of a group of two to four radiating zooids joined at their proximal ends (see below, p. 367).

   Zooids are small and elongate pyriform in shape, narrow proximally and broadening distally to attain their maximum width at about two-thirds the length of the zooid. Well-preserved frontal walls are smooth and lack pseudopores (Fig. 2B); weathered frontal walls have a microstructural fabric parallel to the length of the zooid. The terminal aperture is circular or subcircular and small (*c.* 0·07 mm in diameter). Peristomes are rarely preserved and when present (e.g. in a hollow on the substratum of BMNH PD6023) they are slight and inclined somewhat distally. A poorly-defined zone of modest astogenetic change in zooid length may occur outwards from the early stages of growth (Fig. 3). In BMNH PD6023, but not in NGS 256, the first zooid in each daughter branch is longer than usual, averaging 0·54 mm, compared to 0·44 mm for zooids in the colony as a whole.

Table 1 Zooid dimensions in *Corynotrypa thomasi* Condra & Elias, and *C. voigtiana* (King). Abbreviations: $\bar{x}$ = mean value (mm); SD = standard deviation (mm); CV = coefficient of variation; r = observed range (mm); Nc = number of colonies (*either 2 or 5 colonies of *C. thomasi* were measured depending on whether the holotype specimen comprises a single fragmented colony or several colonies); Nz = number of zooids. Values of zooid width in the holotype specimen of *C. voigtiana* (see Taylor 1980) are excluded because diagenetic crystal overgrowth has increased the measured value of this dimension.

		$\bar{x}$	SD	CV	r	Nc	Nz
C. thomasi	length	0·44	0·047	10·7	0·32–0·62	2–5*	102
	width	0·15	0·010	6·5	0·12–0·17	2–5*	97
C. voigtiana	length	0·50	0·071	14·3	0·39–0·78	8	82
	width	0·17	0·019	11·4	0·14–0·23	7	71

DIMENSIONS. See Table 1.

REMARKS. The holotype specimen (NGS 256) consists of a shell encrusted by one large colony (Condra & Elias 1944: pl. 91, fig. 2) and several isolated, small groups of zooids, some preserving apparent colony origins (Fig. 1C). These small groups of zooids are interpreted as regenerated fragments of the larger colony (see below, p. 369). If this interpretation is correct, the large and small colonies together constitute a clone which might be regarded in its entirety as the holotype of the species.

Corynotrypa voigtiana (King 1850)

1848 *Stomatopora (Aulopora) dichotoma* Lamouroux; King: 6.
1850 *Aulopora Voigtiana* King: 31; pl. 3, fig. 13.
1857 *Hippothoa Voigtiana* (King) Kirkby: 217; pl. 7, figs 14–15.
1858 *Hippothoa Voigtiana* (King); Kirkby: 291; pl. 12, figs 14–15.
1861 *Hippothoa Voigtiana* (King); Geinitz: 120; pl. 20, figs 24–25.
1865 *Hippothoa Voigtiana* Kirkby [*sic*]; Schauroth: 29; pl. 1, fig. 3.
1977 *Hippothoa* ? *voigtiana* (King); Patttison: 36.
1980 *Stomatopora voigtiana* (King) Taylor: 621; fig. 1.

LECTOTYPE. UCG, King Collection B132. Middle Magnesian Limestone Reef, Upper Permian. Humbledon, Sunderland, Tyne and Wear. Colony of 16 zooids encrusting the exterior of a *Horridonia horrida*. Though King's description (1850) implies that more than one specimen of *C. voigtiana* was available to him, this is the only known syntype and was designated as the lectotype by Taylor (1980).

OTHER MATERIAL. BMNH PD6224–6. 'Middle Zechstein', Upper Permian. Pössneck, E. Germany. Presented by J. E. Lee 1885. Colonies encrusting crinoid columnals originally registered as part of BMNH E.1120.

NMC, Schauroth Collection 3541. Zechstein Dolomite, Upper Permian. Pössneck, E. Germany. Several bryozoan-encrusted crinoid columnals are registered under this number, including three better-preserved specimens here suffixed a, b and c (a and c are each fragmented into two pieces). It is not possible to match any of these specimens with Schauroth's (1865) sketchy illustration.

The specimen figured by Geinitz (1861) was amongst those from his collection in the Staatliches Museum für Mineralogie und Geologie zu Dresden destroyed during the Second World War (A. Prescher *in litt.*, March 1983).

Kirkby (1857, 1858) described several colonies from the Magnesian Limestone of Tunstall Hill in Sunderland. The whereabouts of these specimens is unknown; they could not be found among other Kirkby material in the collections of the Hancock Museum, Newcastle-upon-Tyne (A. M. Tynan *in litt.*, September 1983).
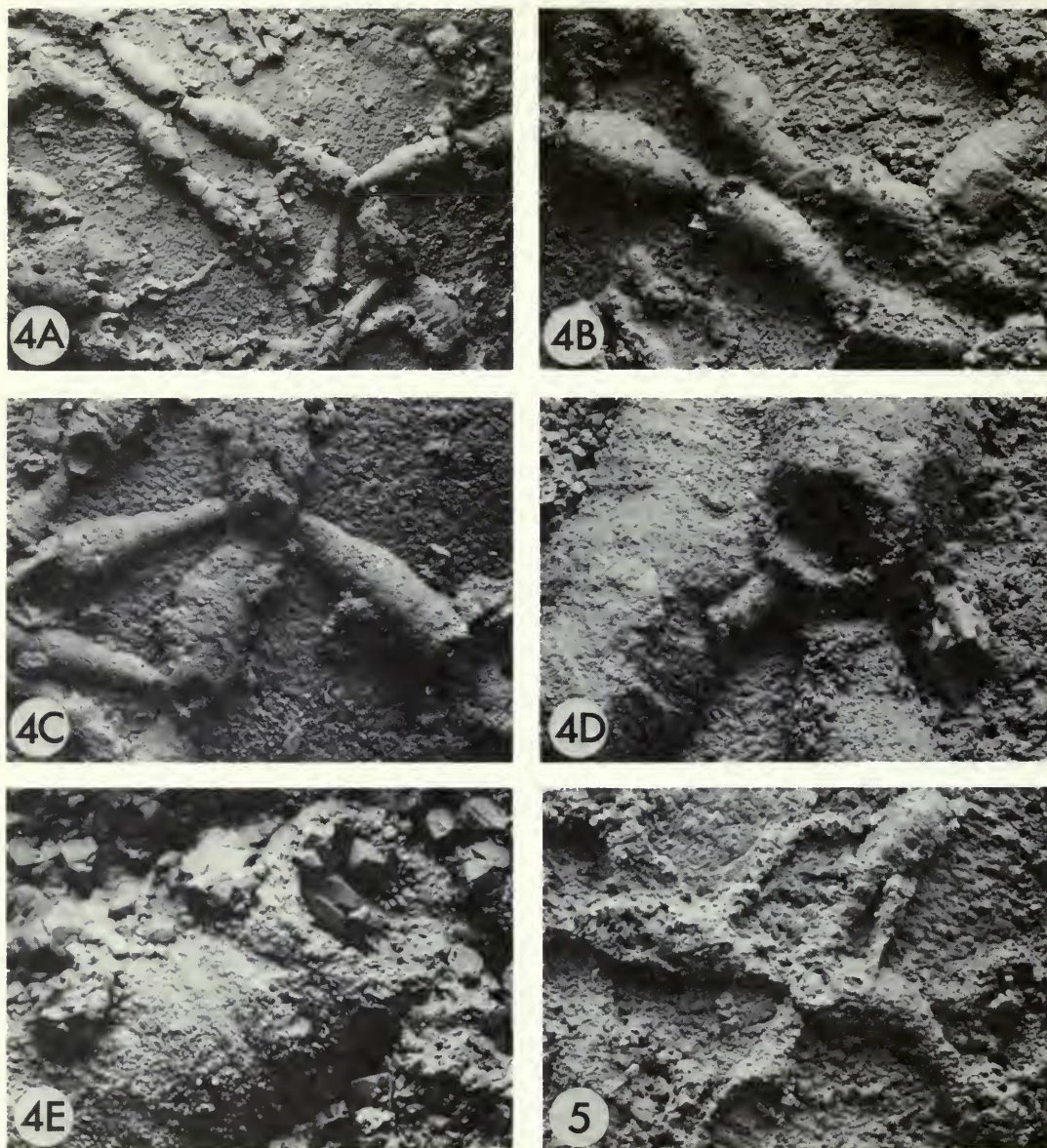
Figs 4–5   *Corynotrypa voigtiana* (King). 'Middle Zechstein', U. Permian; Pössneck, E. Germany. Fig. 4, BMNH PD6226. 4A, zooids encrusting a crinoid columnal, × 28; 4B, two subparallel branches, × 52; 4C, distolaterally-budded zooids initiating lateral branches with narrower proximal parts than distally-budded zooids, × 66; 4D, incompletely formed bud (kenozooid) terminating against the side of an existing zooid, × 160; 4E, zooidal aperture and non-pseudoporous frontal wall, × 260. Fig. 5, BMNH PD6225, typical poorly-preserved colony showing curved zooids and paired lateral branches, × 58.

DESCRIPTION. Colonies are encrusting and consist of branches of uniserially-arranged zooids (Fig. 4A, B). Branches may be gently curved. Daughter lateral branches arise as distolateral buds from zooids on a parent branch (Fig. 4C). These branches diverge from the parent branch at between 60° and 90° and may be paired, one either side of the parent branch. Branching frequency is variable; in some colonies (e.g. UCG B132) fewer than 15% of

zooids give rise to a lateral branch, whereas in others (e.g. NMC 3541a) about 40% of zooids give rise to a lateral branch. Crowding of branches may occur with numerous branch intersections, most resulting in the younger branch abutting against the side of the older branch without overgrowth (cf. Gardiner & Taylor 1982). Very short zooids without apertures are present at some branch intersections (Fig. 4D). These are presumed to be kenozooids resulting from restriction of growth. An apparent colony origin present in NMC 3541c (Fig. 8) consists of two zooids joined at their narrow proximal ends and growing in opposite directions.

Zooids are small and elongate pyriform in shape, attaining their maximum width generally about two-thirds the distance along their lengths. Proximal parts of zooids are especially narrow in the distolaterally-budded zooids that form the first zooids in the lateral branches (Fig. 4C). Some zooids are curved and distinctly asymmetrical. A few straggly zooids are present in BMNH PD6226 and may be abortive. Well-preserved frontal walls lack pseudopores and are marked by transverse wrinkles (Fig. 4D). Frontal walls are commonly poorly preserved and crystalline (Fig. 5). Zooidal apertures are terminal, circular or elliptical and transversely elongate, and small ($c.\,0.06–0.08$ mm in diameter). Peristomes have not been observed. Regular astogenetic variation in zooid size has not been detected.

DIMENSIONS. See Table 1.

REMARKS. An earlier revision (Taylor 1980) of this species was based on a restudy of the lectotype, the only specimen known to be in existence at that time. In this specimen coarse preservation obscures details of wall structure and the presence or absence of pseudopores could not be established. The comparatively broad proximal ends of the zooids (probably due to diagenetic crystal overgrowth) led to the species being incorrectly assigned to *Stomatopora* Bronn. Newly available material shows very clearly the absence of pseudopores in well-preserved frontal walls and the narrow proximal ends of the zooids; these features allow reassignment to *Corynotrypa* Bassler. This new material first came to light among specimens borrowed from the Schauroth Collection in the NMC; they were found encrusting columnals of *Cyathocrinus* from the Zechstein of Pössneck. Examination of crinoid columnals from the same locality in the Echinoderm Collection of the BMNH led to the discovery of three further colonies (BMNH PD6224–6) of *C. voigtiana*, including an especially well-preserved colony (PD6226).

C. voigtiana is very similar to *C. thomasi* but can be distinguished by the slightly longer and wider zooids (Table 1), which may be transversely wrinkled. Lateral branches are more frequent in most *C. voigtiana* colonies.

Propagation in *Corynotrypa*

Sexual reproduction in bryozoans results in free-swimming larvae whose settlement on a firm substrate is the first stage in the formation of the majority of colonies. The founder zooid of these sexually-produced colonies, the ancestrula, is usually smaller than later zooids and may be morphologically distinctive. The ancestrula in *Corynotrypa* has not been illustrated previously, though Dzik (1981: text-fig. 7a) gives an outline diagram of a partly-preserved ancestrula in *C.* cf. *schucherti* Bassler. Dzik (1981: text-fig. 4b) also figures the ancestrula of the related genus *Wolinella* Dzik which has a bulb-like proximal end, the protoecium (= proancestrula, primary disc or basal disc). Protoecia are a feature of the ancestrula in most or all stenolaemate bryozoans and may be a useful skeletal synapomorphy for the Class Stenolaemata. Examination of numerous Ordovician to Permian species of *Corynotrypa* in the BMNH collections has revealed only two examples of zooids that could be positively identified as ancestrulae by the presence of a protoecium. Both are in colonies of *C. dissimilis* (Vine) from the Silurian (BMNH R1900a, D36468). The protoecium in *C. dissimilis* (Figs 10, 11) is somewhat wider than the remainder of the ancestrula and resembles protoecia in post-Palaeozoic cyclostomes (e.g. Gardiner & Taylor 1982: fig. 1A).
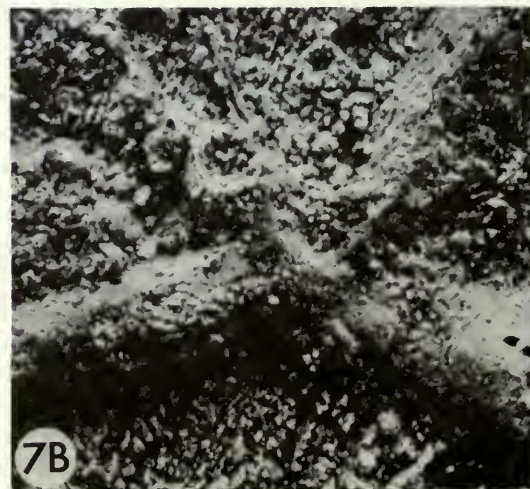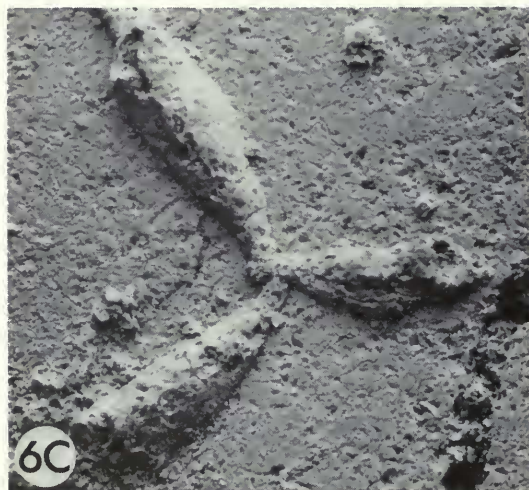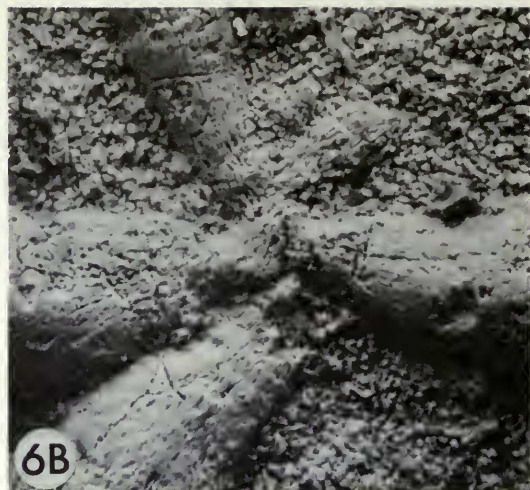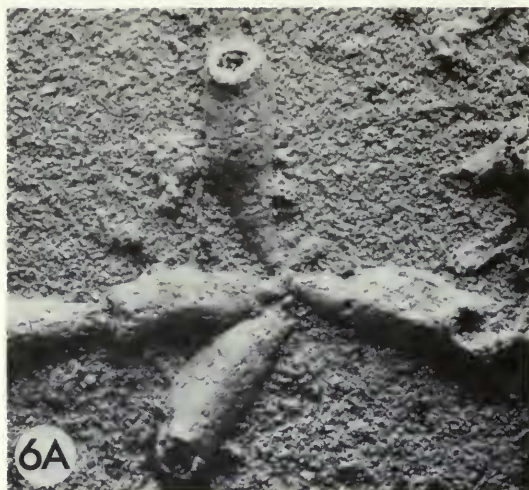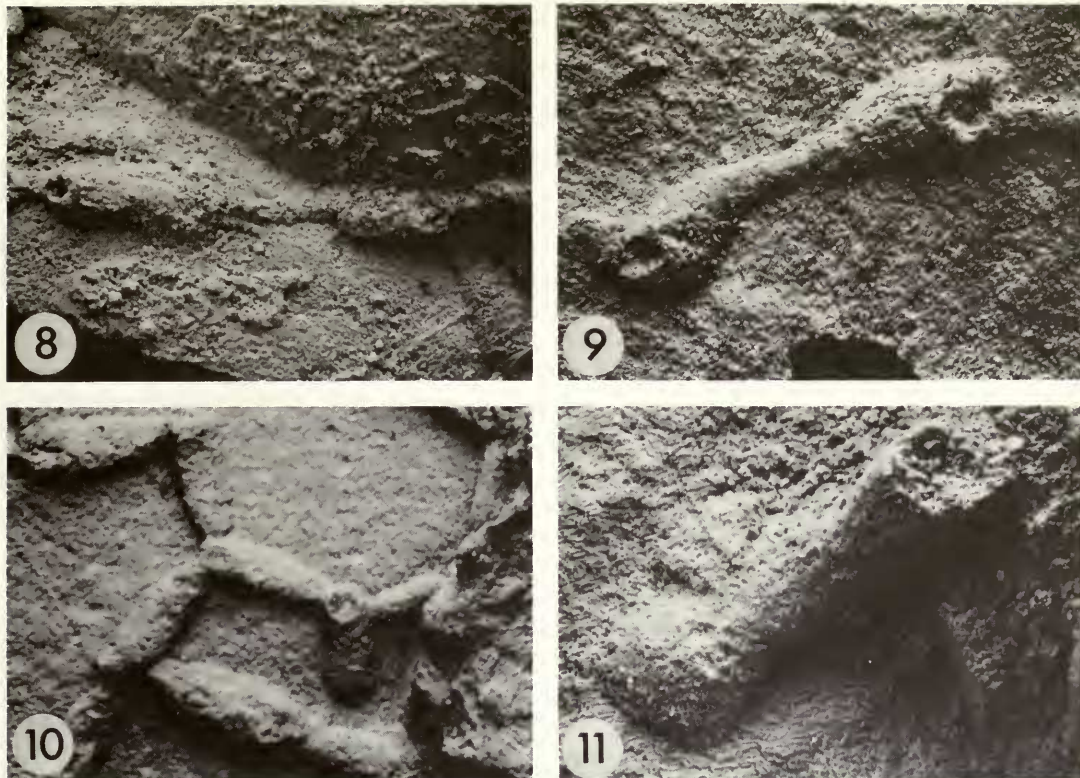
Figs 8–11 Origins of colony growth and ancestrulae in *Corynotrypa*. Fig. 8, *C. voigtiana* (King), NMC Schauroth Collection 3541c; Zechstein Dolomite, Upper Permian; Pössneck, E. Germany. Two zooids growing in opposite directions, × 52. Fig. 9, *C. inflatà* (Hall), BMNH D5851a; Lorraine Group, U. Ordovician; Cincinnati, Ohio, U.S.A. Two zooids growing in opposite directions, × 54. Fig. 10, *C. dissimilis* (Vine), BMNH D36468; U. Silurian; Gotland. Ancestrula with protoecium just right of centre, × 20. Fig. 11, *C. dissimilis* (Vine), BMNH R1900a; Wenlock Limestone, Silurian; Dudley, England. Ancestrula with long peristome and bulbous protoecium (lower left), × 67.

Ancestrulae with protoecia could not be located in most species of *Corynotrypa*, despite the fact that encrusting colonies of *Corynotrypa* are unlike many erect bryozoans in which proximal parts are overgrown by later zooids or can be dissociated from the bulk of the colony prior to burial. When identifiable, apparent colony origins were instead represented by a group of 2–4 diverging or radiating zooids joined at their narrow proximal ends (Figs 6–9). Structures of this type were found in *Corynotrypa* sp. from the M. Ordovician of

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Figs 6–7 Origins of colony growth in *Corynotrypa thomasi* Condra & Elias. Fig. 6, NGS 256; Spring Branch Limestone Member, Lecompton Formation, Shawnee Group, Pennsylvanian (U. Carboniferous); Snyderville Quarry, Nehawka, Nebraska, U.S.A. 6A, group of four radiating zooids at the origin of the large colony shown in Fig. 1A, × 60; 6B, detail of central area showing irregularities, fracturing, and the presence of an additional partial zooid (upper right), × 150; 6C, group of three zooids at the origin of the small colony shown in Fig. 1C; × 72; 6D, detail of central area showing broken proximal end of zooid on the right which has apparently formed two proximolateral buds, × 210. Fig. 7, BMNH PD6023; Bangor Limestone (lower), Chesterian, Mississippian (L. Carboniferous); Fox Trap, Colbert County, Alabama, U.S.A. 7A, group of three radiating zooids at the origin of colony growth, × 67; 7B, detail of central area showing open proximal end of the smallest of these three zooids, × 330.

Virginia (BMNH PD5776), *C. inflata* (Hall) from the U. Ordovician of Cincinnati (BMNH D5851a, Fig. 9), *C. dissimilis* from the Silurian of England (BMNH 60521), *C. thomasi* (Figs 6, 7) and *C. voigtiana* (Fig. 8). Initially it was thought that one zooid within each group was the ancestrula or, alternatively, that the group as a whole constituted an ancestrular complex. However, the lack of a protoecium is evidence against both of these interpretations. Ancestrular complexes, known in several cheilostomes (Cook 1973), are as yet undescribed from stenolaemates (though more than one zooid may bud from the protoecium in some cyclostomes, Illies 1974), and the variability in the number of zooids (2–4) comprising the group in *C. thomasi* does not match with expectations for an ancestrular complex. Finally, the occurrence of these apparent colony origins in a species (*C. dissimilis*) known to have an ancestrula with a protoecium demonstrates that, in this species at least, none of the radiating zooids is the ancestrula. Detailed scanning electron microscope (SEM) studies revealed growth irregularities at the loci of the groups of radiating zooids. There are indications of fracturing at the proximal ends of the zooids, and short, broken segments of additional zooids may be present (Fig. 6B). This suggests that these colony origins represent damaged parts of colonies repaired by regenerative budding of zooids in proximal and other directions. Similar structures have been described in the uniserial cheilostome *Pyriporopsis*? *catenularia* (see Cheetham & Cook *in* Boardman *et al.* 1983: figs 76, 1a). The growth pattern
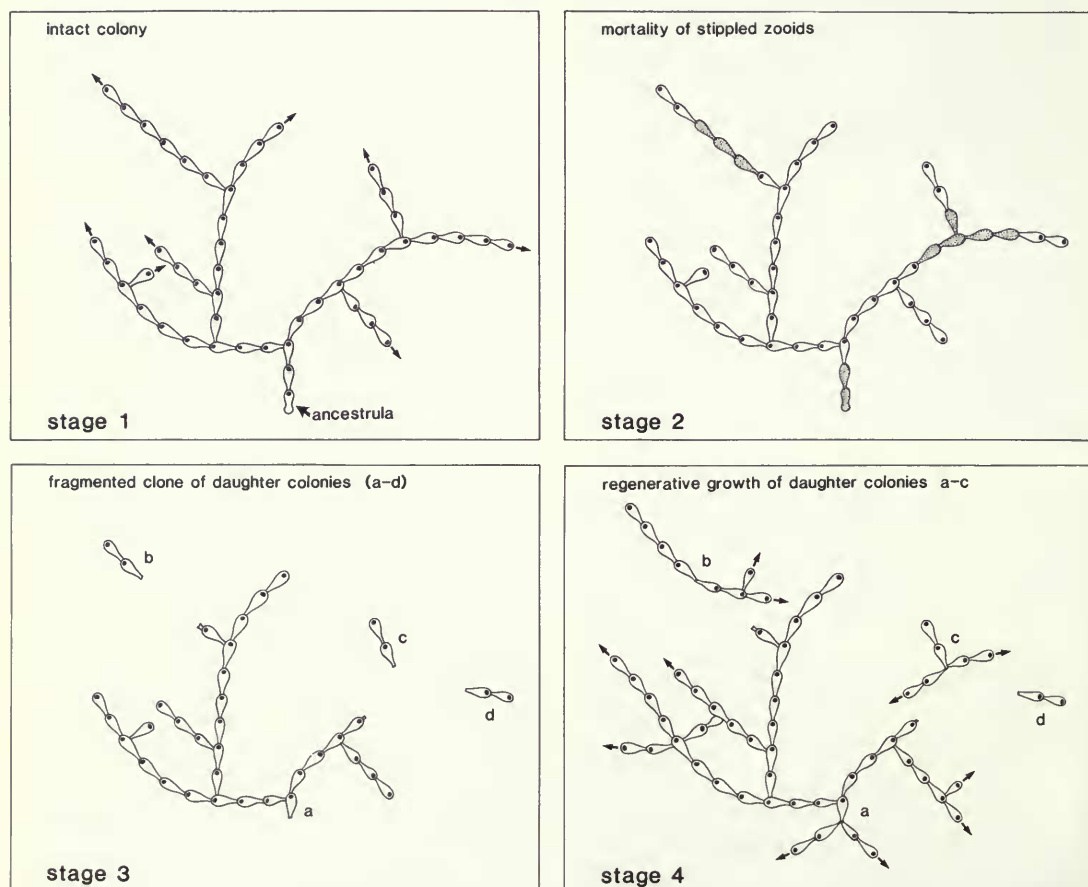

Fig. 12 Model of clonal propagation by colony fragmentation in *Corynotrypa*. Arrows indicate active growing tips.

of *P.? catenularia* colonies closely resembles that of *Corynotrypa* and, as in *Corynotrypa*, the ancestrula is unknown; a possible ancestrula in *P.? catenularia* figured by Cheetham & Cook (*in* Boardman *et al.* 1983: fig. 76, 5) proved, when examined using SEM, to have irregularities suggestive of fracturing and repair.

Encrusting colonies of *Pyriporopsis?* and *Corynotrypa* have runner-like growth forms well suited to the location of spatial refuges on the substrate (Buss 1979, Jackson 1979). However, such fugitive colonies are likely to be poorly committed to the defence of individual zooids within the colony. Therefore, zooids may be highly ephemeral. This would have two consequences: firstly, there would be a low probability of the earliest zooids (including the ancestrula) remaining intact in old, large colonies; and secondly, fractured branches, at least some of which might be repaired, would be of frequent occurrence.

The holotype specimen of *Corynotrypa thomasi* consists of a shell encrusted by a large colony (Fig. 1A), and several isolated small colonies each comprising only a few zooids (Fig. 1C). Some of these small colonies originate from groups of radiating zooids of the kind interpreted as products of regeneration following damage. It seems probable that these small colonies are ramets (*sensu* Harper 1977) formed by fragmentation of the larger colony. Fig. 12 depicts diagrammatically the fragmentation process envisaged. While some of the fragments may have ceased growth, others evidently retained viability and, in addition to resuming normal distal budding, were able to produce proximally growing buds to repair their fractured proximal parts. Fragmentation is presumed to have been caused by external agencies among which grazing of the substratum surface could have been important (cf. Jackson & Winston 1981).

Recent interest has been shown in fragmentation as a means of asexual or clonal propagation in colonial animals (e.g. Highsmith 1982, Hughes 1983). Clonal propagation in bryozoans seems to be associated mainly with erect and free-living colonies (e.g. Marcus & Marcus 1962, McKinney 1983, Winston 1983 and Hakannson & Thomsen in press – paper presented at the 6th Conference of the International Bryozoology Association, Vienna, July 1983). Jackson & Winston (1981), however, describe examples of colony fission in encrusting cheilostomes on fouling panels placed on Caribbean reefs. In erect and free-living bryozoans
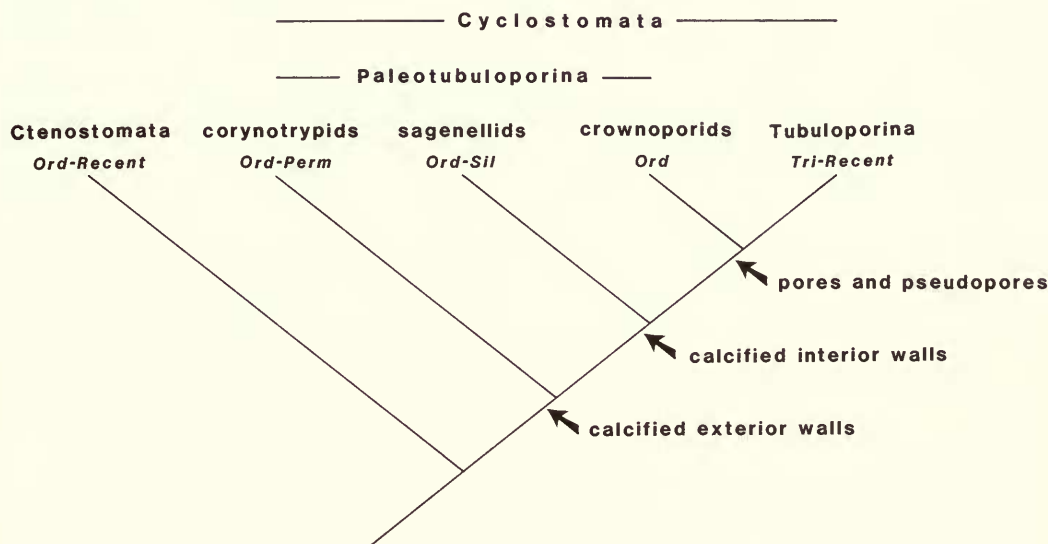

Fig. 13 Tentative, simplified cladogram showing inferred relationships between Palaeozoic cyclostomes and primitive post-Palaeozoic cyclostomes (Tubuloporina). The Ctenostomata are regarded as the primitive sister group of the Cyclostomata (see Larwood & Taylor 1979).

the individual fragments (daughter colonies) of the clone commonly become spatially separated after breakage. Here clonal propagation can have a role in dispersal, colonization of virgin environments, and increasing genotype longevity. Except in cases where the substratum itself is broken and the fragments separated, clonal propagation in encrusting bryozoans would appear to have no significance in these roles. Instead it seems merely to be a consequence of the ability of colonies to survive fission. Nevertheless, recognizing the possibility of clonal propagation in encrusters such as *Corynotrypa* is of importance during studies of population abundance, overgrowth relationships, between colony morphological variation, etc.

Remarks on phylogeny

In the only major studies, Palaeozoic cyclostomes have been classified within the Suborder Paleotubuloporina Brood, 1973 (Brood 1973, 1975; Dzik 1981). However, the morphological basis of this suborder is unclear. Brood's original diagnosis (Brood 1973) emphasizes the absence of interzooidal pores and pseudopores (though pseudopore-like structures were described in one genus), whereas Dzik's amended diagnosis (Dzik 1981) stresses the presence of interzooidal pores ('communication canals').

A review of existing morphological descriptions suggests that Palaeozoic cyclostomes divide into three informal groups: corynotrypids, sagenellids and crownoporids. These correspond approximately to the families Corynotrypidae Dzik, 1981, Sagenellidae Brood, 1975 (excluding *Corynotrypa*) and Crownoporidae Ross, 1967 (= Kukersellidae Brood, 1975 which was incorrectly proposed to replace Crownoporidae following the recognition of *Crownopora* Ross, 1967 as a subjective junior synonym of *Kukersella* Toots, 1952). Corynotrypids lack calcified interior walls and consequently have complete continuity between the zooecial chambers of contiguous zooids; sagenellids have calcified interior walls separating contiguous zooids but these walls are non-porous and the exterior walls lack pseudopores (the paired frontal pores of *Sagenella consimilis* (Lonsdale) are probably not pseudopores); crownoporids have calcified interior walls with pores and/or exterior walls with pseudopores.

Of the three groups of Palaeozoic cyclostomes, crownoporids most closely and corynotrypids least closely resemble post-Palaeozoic cyclostomes. Although there are broad similarities in colony-form and zooid shape between many corynotrypids and primitive Mesozoic stomatoporids, these similarities may be poor indicators of phylogenetic affinity. Stomatoporids differ from corynotrypids in having well-developed calcified interior walls with pores, and exterior walls with pseudopores. In all Jurassic stomatoporids branch multiplication occurs by bifurcation and not lateral branching as in corynotrypids. Regenerative proximal budding of zooids has not been observed in Jurassic stomatoporids. Therefore, evolution of primitive post-Palaeozoic cyclostomes from a late Palaeozoic corynotrypid like *Corynotrypa voigtiana* seems unlikely. Primitive post-Palaeozoic cyclostomes may have closer affinities with crownoporids with which they share porous interior walls and pseudoporous exterior walls (Dzik 1981). These similarities are assumed to be homologous (synapomorphies) rather than convergent, though knowledge of crownoporid morphology is deficient and the group may encompass a wide variety of morphologies. Favoured relationships are expressed in a tentative cladogram (Fig. 13). A problem of this hypothesis of relationships is the large hiatus in the fossil record between crownoporids, which are possibly restricted to the Ordovician, and the first post-Palaeozoic cyclostomes which appear in the late Triassic (Prantl 1938, Bizzarini & Braga 1981). Poor preservation potential may partly explain this gap. Palaeozoic cyclostomes have thin colonies that contrast with those of the other Palaeozoic stenolaemate orders. These thin colonies are both delicate and easily overlooked. Therefore resolution of phylogenetic relationships should be clarified not only by more complete morphological study of known species, but also by the search for further encrusting cyclostomes attached to shell substrates and erect cyclostomes within fine-grained sediments.

Acknowledgements

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